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EVOLUTION AND MUTATION.

IN the beginning of the last century Lamarck founded the theory of a common descent for all living beings. It afforded him the only possible means of explaining systematic affinity. He assumed that the influence of the environment was capable of changing the characters of the organisms, and of fitting them for their life-conditions. His evidence, however, was very scanty and therefore he failed in convincing his contemporaries.

Half a century afterward Darwin brought together such an overwhelming mass of evidence that opposition had to give in. His main point was one of comparative investigation. At his time it was universally assumed that species had been created as such, but that subspecies and varieties had been derived from them according to natural laws. Darwin proved that no such distinction between species and subspecies exists. Their marks are of the same nature, and if a natural origin is assumed for one group, it must be conceded for the other, too. The same holds good for genera and families, and even for the higher divisions of the system.

Moreover, Darwin showed that the sequence of the appearance of organisms during geological times finds a natural explanation on the assumption of the theory of descent, and that the geographical distribution of animals and plants is exactly as we should expect it to be if their common origin were the main factor in assigning them their special domains.

These broad proofs of the theory of evolution are quite independent of the question by which means and in what way new species are produced from the existing ones. This question, however, appeals more directly to the imagination and Darwin collected all the evidence concerning it which he could find. The rapid victory gained by his views has been due mainly to his discussion of this minor point.

Direct observations concerning the first appearance of species in nature were not at hand. In agriculture and in horticulture, however, numerous observations had been made, and for a number of races and varieties the origin was historically known. Distinct methods were in use to guide these changes and to produce varieties which would comply with the demands of practice. The grand principle of all these methods was selection. Selection means guiding the changes in the specific characters of organisms by cutting off all those which are changing in undesirable ways, and reserving for reproduction only those which differ advantageously from the average.

Darwin proved that the origin of species in nature must be the same phenomenon as the origin of races and varieties in culture. He showed that in nature an analogous process of selection is steadily active. More seeds are produced and more children are born than can possibly survive, and the decision as to which are to live and which must die, depends, on one side, on the life-conditions and, on the other, on the distinctive qualities of the competing individuals. Of course, in the single instances survival depends mainly on chance, but in the long run the different chances may be assumed to annul each other's influence, and the decision falls to individual excellences and life-conditions. In this way the latter can be said to make a choice of the individuals best fitted for the local conditions and this is what is now universally known as *the principle of natural selection.* It guides evolution, keeping it in the useful ways, and destroys all that try to diverge in opposite directions.

The theory of common descent is Darwin's theory, since it has been founded by him on so broad a basis of facts as to insure almost universal acceptance. The theory of natural selection is one of the means by which this position has been reached. It is the application of the breeding practice to the phenomena of nature at large. Darwin's theory is often designated as the theory of natural selection. This is, however, not the same as the theory of descent. The idea of descent with modification, which now is the basis of all evolutionary science, is quite independent of the question as to how, in the single instances, the change of one species into another has actually taken place. The theory of descent remains unshaken even if our conception concerning the mode of descent should prove to be in need of revision.

Such a revision has become necessary by the gradual development of the study of variability. Darwin has demonstrated that all the individuals of a given species differ from one another to some extent, and that many of these differences increase or lessen their chances of survival. A struggle for life ensues and, sooner or later, the unfit individuals succumb, thereby leaving the average of the species changed to some slight degree. Differences between isolated local races afford the means of studying the efficiency of this process of variability and selection. The question arises, however, as to how far this variability may go under the influence of this guidance. Is it limited or unlimited? Can it proceed during centuries and in the same direction, augmenting the differences to any extent, or is it bound by its original average condition, without being able to diverge far from it? Can it produce new characters and new qualities or is it limited to changes of degree in those that already exist? To all these and many other questions, an answer could not be given at the time of Darwin, the evidence being too incomplete. It was, however, necessary to make a decision of some kind, and thus it was universally assumed that the changes by which species originate are slow, almost invisible, and may accumulate, in the lapse of time, to any degree. All of the characters of living organisms were simply assumed to be due to this slow process of gradual evolution guided by natural selection.

Here, however, a first difficulty arose. We do not observe actual specific changes in nature. To meet this objection Darwin assumed the changes to be so slow as to be invisible to us. Even the life-time of a man would not be sufficient to control them. By this supposition the evolution of a flower or a seed or of highly differentiated organs (such as the leaves of insectivorous plants) would require an enormous time. From this a calculation could be made as to the time required for the whole range of evolution of the vegetable and animal kingdoms. The result was that many thousands of millions of years were considered to be the smallest amount that would account for the development of life on earth from the very first beginning until the appearance of mankind.

Physicists and astronomers have objected to this conclusion. The objection has been brought forward from the time when Darwin published his calculation. It has never relented and has often threatened to impair the whole theory of descent. The results of physical and astronomical calculations concerning the age of life on this earth differ so widely from the demands made by the theory of slow evolution as to be considered incompatible with them. The deductions made by Lord Kelvin and others, from the central heat of the earth, from the rate of the production of the calcareous deposits, from the increase of the amount of salt in the water of the seas and from various other sources, indicate an age for the inhabitable surface of the earth of between twenty and forty millions of years only. This large discrepancy has always been a weapon in the hands of the opponents of the evolutionary idea, and there can be no doubt that it proves that the current view of extremely slow and almost invisible changes must be abandoned.

Shortly after the publication of Darwin's *Origin of Species,* the Belgian anthropologist Quetelet submitted the variability in measurement of the different parts of the human body to a statistical investigation. He discovered that this kind of variability follows distinct laws and that these laws agree, in the main, with the law of probability. Small divergences from the average are numerous, larger discrepancies are rare, and the rarer, the larger they are. Variability is thereby limited, and is subject to a return to the average condition. It may be moved from this average, to some extent, by a change in the outward conditions or by a repeated selection in one direction; but, as soon as these causes and this selection cease to work, a return to the average is unavoidable. Variability may augment or diminish the qualities; it is linear, consisting of changes along a simple line, some being positive and others negative, but it does not strike into new directions. It is no source of new qualities. The phenomena which are controlled by this law and which are bound to such narrow limits cannot be a basis for the explanation of the origin of species. It governs quantities and degrees of qualities, but not the qualities themselves. Species, however, are not, in the main, distinguished from their allies by quantities or by degrees—their very qualities may differ.

From this discussion it may be seen that the slow and gradual changes of ordinary variability and the production of new characters are not of the same order. Variability, in the ordinary sense of the word, is a broad conception. It must be subdivided for the purpose of scientific investigation. The phenomena that follow Quetelet's law are now considered as one group, which is called fluctuating variability or fluctuation, since the individual qualities fluctuate around their average. The processes by which new qualities are produced must be studied separately. Under the assumption that these processes are neither slow nor invisible, but consist in leaps and jumps such as are popularly indicated by the name of sports, they are now called mutations, and this great subdivision of the phenomena of variability is designated, in consequence thereof, as mutability.

Darwin was well aware of the existence of different cases of variability, and of the possibility of their bearing on the theory of evolution. He considered the assumption of an origin of species in nature by leaps and sports, such as were observed to occur among horticultural plants. He pointed out that the affinity of closely allied species can be explained on this assumption as well as by slow changes. If we consider all the varieties and subspecies of apples, or beets, or of one of the cereals, and assume thousands of years for their production, the changes may have been brought about by rare sports as well as by long continued changes: the effect, at the present time, would be the same. Darwin agreed that this possibility could not be denied and that it was a very weak point in his hypothesis of slow evolution.

The mutations must not be assumed to be considerable changes. From a study of the differences among small species we may form some conclusion as to their probable size. Common observation shows the difference between allied species, ordinarily, to be quite striking; but a little discussion and a closer inspection will easily prove that, in such cases, the differences are due to more than one, and often to numerous, characters. In groups, (such as brambles, roses, buttercups, willows and many others) where large numbers of species are closely allied, the differences between any two of them become smaller and the number of distinct forms increasing, the distinction, in the end, may be reduced to one single differential mark for each two neighboring types. Such differences must be assumed to be produced each by a single mutation. By this means the significance of the mutations may best be judged, and whenever species differ from their nearest allies in a higher degree, the inference is allowed that they have been originated by more than one mutation.

Since the publication of Darwin's theory, the probability of such sudden changes playing an important part in the evolution of species has always found some support. Of late, the evidence has increased in this direction, especially under the influence of Cope. Discontinuous evolution has been defended among palæontologists by Dollo, among zoölogists by Bateson and among botanists by Korshinsky. This Russian author compiled the history of a large number of varieties from the widely scattered horticultural literature and showed that, in almost all cases where the history of the origin of a variety was recorded, it originated suddenly. Many other varieties, especially among trees and shrubs, have been discovered as such in the field, and although their origin is not historically known, the constant absence of intermediates pleads vigorously for the explanation of their differential qualities by mutation.

The conception of mutations agrees with the old view of the constancy of species. This theory assumes that each species has its birth, its life-time and its death even as an individual, and that throughout its life it remains one and the same. Thus it is only natural that wild species are almost always observed to be constant, since by a mutation they do not change themselves but simply produce a new type. This is allied to its ancestor as a branch is to a tree, the stem continuing its own growth, no matter how many branches it produces. Just so a species may produce quite a number of new forms without being changed itself in the least thereby. Among palæontologists Scott has given forth this same view. According to his conception, species are derived from one another by small shocks. Each shock caused the old limits to be transgressed; but, after it, the new species remained unchanged until, perhaps after centuries, a new shock made it transgress its new limits. Each single type (be it species, subspecies or variety) is thus wholly constant from its first appearance and until the time it disappears, either after, or without, the production of daughter-species.

On the ground of the mutation-theory there is a struggle for life among species as well as among individuals. There is selection, also, between competing species and between the individuals of the same species: the fittest will survive,—but this holds good for species as well as for individuals. As to individuals, natural selection may, to some extent, cause a divergence from the average type. But among species natural selection is the most potent factor, since it eliminates some and thereby protects and favors others. Thus we come to the conclusion that natural selection is as active as Darwin assumed it to be, and is as pre-eminent a factor in the process of evolution. It causes the survival of the fittest; but it is not the survival of the fittest individuals, but that of the fittest species, by which it guides the development of the animal and vegetable kingdoms.

Resuming the main points of this discussion, we may sketch the origin of species, according to the theory of mutation, in the following manner. Species are derived from other species by means of sudden small changes which, in some instances, may be scarcely perceptible to the inexperienced eye. From their first appearance they are uniform and constant, when propagated by seed; they are not connected with the parent species by intermediates and have no period of slow development before they reach the full display of their characters. They do not always arise, but only from time to time. A parent-species may produce its offspring separately at intervals or in larger numbers during distinct mutating periods. After this production, the old species is still the same as it was before and it subsists in the midst of its children. New forms are produced by the old either in one, or a few, or in numerous individuals; in the latter case, the chance of survival is evidently enhanced. Some young species will be better fitted for their life-conditions than others, and the struggle for life will induce a selection among them by which the fittest survive. Even as the new species are produced locally and as the effect of local causes, the struggle for life and natural selection decide concerning the survival according to the local conditions. These conditions thus have a twofold significance for the development of the pedigree of the main groups of plants and animals, but it is probable that they determine the lines of progress chiefly by their selective activity.

The main arguments in the discussion of the production of species by slow changes or by mutations were taken by Darwin from the experience of agricultural and horticultural breeders. Therefore it is desirable to inquire into their real significance. Do they support the one or the other view? Darwin assumed that they gave proof of slow changes, and took his arguments mainly from the agricultural side. In horticulture, however, as we have seen in discussing Korshinsky's work, the probability is on the other side. In my experiments on mutability I have shown that it is possible to repeat and control the origin of horticultural and analogous varieties under strict experimental precautions, and that the full proof may be given that they originate at once and not by a slow process of changes. They may, in the first instance, appear with the full display of their average character, or only with a small indication of it as an extreme variant of its fluctuation, but in the latter case the average is often reached after one more generation.

I observed the origin of the peloric toadflax and of a double marigold and produced, almost artificially, the twisted variety of a Dracocephalum.

In the case of the toadflax, *Linaria vulgaris peloria*, the change came suddenly, and more or less unsuspectedly, after a culture of about eight years. The ordinary form produces, from time to time, some few five-spurred, regular or peloric flowers. At once an individual arose which had such flowers only. The next year the mutation was repeated. The seeds of the mutated individuals reproduced the new variety almost exclusively, and each plant of it had peloric flowers only. No intermediates were observed, neither in the number of the spurs of the flower, nor in the number of peloric flowers on the plants. It was as sudden a change as any horticultural sport, but its ancestry had been purely fertilized and carefully recorded so as to leave no doubt concerning the real nature of the mutation.

The double variety of the corn-marigold (*Chrysanthemum segetum*) arose in my garden in a culture in which I was increasing the number of ray-florets by continuous selection. During four years I had succeeded in increasing this number to about sixty on each head, starting from the cultivated variety with an average of twenty-one. All the ray-florets, however, belonged to the outer rows of the heads, as in the original variety. At once a plant arose which produced some few ligulate florets in the midst of the disc. This indicated the production of a double race. When the seeds of this mutating individual were sown the next year, they yielded a uniformly double group; and from this time the new variety remained constant.

The *Dracocephalum moldavicum* is an annual garden-plant belonging to a genus in which Morren has described some beautifully twisted specimens. I succeeded in procuring such a specimen in this species by cultivating a race of it during some few years, selecting the specimens which showed a marked tendency toward variation in the arrangement of their leaves. The twisting appeared at once, but the race has not been continued.

All these, and many other, experiments have been conducted under conditions which allowed of a close scientific study. They confirm the common experience of the horticultural breeder in stating the suddenness of the changes and the immediate production of distinct races. They show us the way in which analogous changes may have occurred in nature and make it probable that sudden changes are, at least, an important factor in the evolution of the vegetable kingdom.

With agricultural crops my experiments have been too rare to give a definite result. The German breeders assumed, as a rule, that they produced their races at will and by a process of slow variability and repeated selection. It is mainly upon this conviction that Darwin has based his conception of an analogous slow improvement of species in nature. This German method has, however, been submitted to a severe criticism by Dr. Nilsson, the Director of the Swedish Agricultural Experiment Station at Svalöf. His pedigree cultures have shown that the idea of a slow accumulation of characters by repeated selection is due to incorrect observations and to the use of untrustworthy methods. According to his experiments, changes occur in agricultural plants as suddenly as in horticultural species; there is no essential difference between them in this respect. By these discoveries the main support of the theory of slow and gradual evolution is broken down and the analogy between artificial and natural production of species comes to plead wholly for the theory of mutation.

The principle of mutations is conducive to the assumption of distinct units in the characters of plants and animals. Even as chemistry has reached its present high development chiefly through the assumption of atoms and molecules as definite units, the qualities of which would be measurable and could be expressed in figures, in the same way systematic botany and the allied comparative studies are in need of a basis for measurement and calculations. The determination of the degree of affinity now largely depends upon vague estimates and personal views; while, on the basis of the theory of mutations, the relationship is measured by the number of the mutations which have made the forms under consideration different from their common ancestors. The mutations themselves have evidently occurred in previous times and cannot be counted now. But if it were possible to count their products, the characters, the same aim could be reached.

The study of these unit-characters may be undertaken in three different ways: first, by the production of hybrids; secondly, by the investigation of associated characters; and, in the third place, by the direct observation of mutations producing such units. In hybrids the characters of the parents may be combined in different ways, but the unit-characters cannot be split or divided. This follows directly from their definition. Thus the different combinations may lead to the distinction of the constituents of the mixture. The experiments of Luther Burbank afford a sufficient source of evidence to discuss this question and are well-deserving of a separate treatment. On the other hand, their methods and scientific results are the same as those of the European horticultural breeders.

The association of characters is often called correlation. It may be an accidental or a normal coincidence of character-units. But more often the same simple character manifests itself in different parts of the organism (as, for instance, in the color of flowers, berries, seeds and foliage) and thereby affords a means of investigating it. Of late, such associations have become of high importance, since selection may be guided by them. Especially in the isolation of new varieties of cereals has this use proven very valuable.

For the direct observation of the process of mutating, the Evening Primrose of Lamarck affords at present an unequaled opportunity. It produces numerous mutants, and does so in every generation, and almost any sample of pure seed may be used for this study. This species was described by Lamarck from specimens of the botanical garden at Paris, a century ago. It seems to have since been lost. It was re-introduced into European garden-culture about the middle of the last century, by a nurseryman in London who received the seed without name and in a mixed packet, cultivated and multiplied it and sold it to the leading firms of the continent. All the strains derived from this source show the same phenomena of mutability, as far as my experiments go. Where the species is growing in America in the wild condition, is not known at present, and so it is impossible to decide whether it has acquired the habit of mutating in that condition or upon its introduction into European culture.

Twenty years ago, I found this species on a waste field near Hilversum, in Holland, where it had escaped from cultivation and was rapidly multiplying. Here it had produced two new and distinct varieties which, up to the present time, have not been collected or observed elsewhere. One of them had smooth leaves, lacking the bubbles of the ordinary form; it was a fine type with narrower leaves and petals, the latter often becoming ovate instead of cordate. The other had very short styles, the stigma reaching only the mouth of the flower-tube, instead of being lifted up above the anthers. Its ovary is only partly inferior, and it ripens only very few seeds in its capsules which remain small. It has, moreover, some associated characters in its foliage by which it may be recognized before the flowering period. In my cultures, both these varieties were found to be constant and pure from seed. Some further mutations have been produced on the same field, but since they were also produced in my experiment garden, I shall not here mention them separately.

In the year 1886 I collected some seed from the normal plants of this field and sowed them in my garden, the next spring. This culture at once gave a new mutation wholly unobserved until that time. Three individuals diverged from the average, and all three in the same way. They constituted a new type which has been called Oenothera lata or the broad-leaved evening primrose. Its leaves have rounded tips, its stems are weak and bending and scarcely reach half the size of those of Lamarck's primrose. It has thick flower-buds and produces flowers, the petals of which often cannot completely flatten themselves. The anthers are barren of pollen, dry and twisted. Its ovary, however, is normal and can easily be fertilized by the pollen of the parent species. In doing so the next generation is, of course, of hybrid origin; but it does not produce intermediates but consists of some typical Oenothera lata and some normal Oenothera Lamarckiana. By repeating the cross the lata-type may be kept indefinitely, occurring in about the same numerical proportion in each generation.

Starting from these mutations, I began a regular scientific pedigree-culture of Lamarck's evening-primrose, fertilizing the flowers artificially with their own pollen, protecting them from the visits of insects by paper bags and sowing, each year, the seeds of some few normal individuals of the race. This pedigree embraces, now, about a dozen generations, the first few of which were biennial, but the later annual. From this stock of normal plants it has regularly repeated its first mutation, producing some latas in almost every generation. The number of these mutants was, on the average, about 1½ per cent., the mutants themselves being always alike.

Moreover, my pedigree-culture has produced quite a number of other mutants. The most frequent among them is a dwarfish variety, the first flowers of which open when the stem is only some few inches high. It is called Oenothera nanella and occurs as frequently as the Oenothera lata. It is completely fertile and produces an abundance of seeds, all of which give the same dwarf type, without ever reverting to the high stature of the parent species. I have cultivated these dwarfs during five and more generations and have found them true to their type.

The first generations of my pedigree-culture had to meet with all the difficulties of a new experiment with unknown and partly unsuspected results. Accordingly, they yielded only a small number of mutants. As soon as the method had been elaborated, this number rapidly increased. In the spring of 1895 I sowed seed enough to have about 14,000 young seedling plants, which I cultivated until they clearly showed whether they had mutated or not. The mutating individuals were then isolated and grown under very favorable conditions, but of the normal plants the larger part were destroyed. All in all, I isolated 60 dwarfs and 73 lata and five wholly different new types. Two of them were rare, one having been found only in one (O. gigas) and the other in two individuals (O. leptocarpa). Two others were less rare, the rubrinervis appearing in eight, and the albida in fifteen specimens. The fifth was the most frequent of them all, springing from the main stem of the Lamarckiana in 176 of the 14,000 seedlings. It was called oblonga. All these forms were purely self-fertilized and yielded uniform races without reversion to the original evening primrose of Lamarck.

With the exception of the gigas, which has not been repeated in this pedigree, all the types spring more or less regularly, in every generation, from the pure parent stock. As often as they were purely fertilized they produced constant strains which, however, did not differ from the previous races of the same name.

Besides these, quite a number of minor mutations have occurred in my cultures. Some of them died in early youth or before flowering; others were barren of pollen, or not capable of fertilization, and yielded no seeds. Some were too weak for the conditions of my garden and succumbed, sooner or later, mostly during the winter after their germination. The range of mutability of this primrose, evidently, has not been exhausted; and even during last summer a wholly new type made its appearance.

A main point in these observations is that the mutations occur suddenly, without preparation and without intermediates. Nothing indicates, on the normal plants, what their seeds will produce and there is even no means at all by which to decide beforehand whether the fruits of one individual, or one branch, will be richer than any other in the production of mutations or of some distinct mutant. The distribution of mutating seeds seems to depend simply upon chance. Nor are there intermediates. Each mutant is as good a representative of its type as its progeny will be; it does not need any special cultivation or improvement to reach the full display of its character. No half-mutants are seen, either from seed of the parent form or from seed of the first mutant itself. These sharp distinctions clearly indicate that each mutation consists of the production of a single unit-character; because, if the characters were compound, they would split, from time to time, and be divided into their constituents. By this means a method is given of studying the expressions which the same unit-character may assume in the different organs of a plant.

The question now arises, whether it must be supposed that species in nature ordinarily originate in the same way as in the case of the evening primroses. Of course, the details of the process will be different in different cases. The number of the new types and the frequency of the mutating individuals in each will differ; sometimes they may, perhaps, be more rare and, in other instances, more crowded. Other differences there will also be. The main point is, however, that mutations occur suddenly and by leaps. One generation is sufficient to produce the whole new type. This is a manifest contrast with the prevailing conception of slow and almost invisible changes producing new species. It may shorten the geological time required for the evolution of the whole living world and bring it within the limits derived from physical and astronomical evidence. The theory of mutation satisfies these demands.

The cases observed in horticulture, the constancy of wild species, the behavior of characters in crosses, the occurrence of sharply defined small species within the ordinary species of wild plants and even of agricultural crops, and many other groups of facts, lead to the same conclusion. On the other hand, the slow change of one species into another has not, as yet, been proven in any distinct and clear case. Therefore, we may assume that the mass of the present evidence points to the conclusion that species originate laterally from other species, by sudden leaps. These leaps we call mutations.

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